NOTES ON SUCCESSION FROM PINE TO OAK BARRINGTON MOORE ...

Recent developments in the study of vegetative succession have changed ideas about the factors causing pine forests and oak forests. Formerly, even after the advent of the dynamic point of view, pine was supposed to grow only on sandy soils and oak only on soils containing clay. Now there is a strong tendency to consider pine as merely an earlier stage in the evolution from simpler associations to the climatic climax of the region, though the effect of the soil in hastening the process of evolution is recognized. The work in the region of the Great Lakes, particularly south of Lake Michigan,¹ has done much to bring this about. The ideas developed by these and other workers are widely disseminated through the literature dealing with vegetation and environment. But TAYLOR² has lately found, on the strength of geological facts which geologists admit are incontrovertible, and of phytogeographic evidence which appears at least convincing, that the pine barrens of New Jersey are not a new, but a very ancient, vegetation.

The attitude toward pine forests, therefore, may have to undergo revision. This does not mean necessarily that the work of COWLES and his associates is in error, but that possibly their conclusions have been too widely applied. It must be remembered that our knowledge of the factors which influence plants, especially of the

¹ COWLES, H. C., The physiographic ecology of Chicago and vicinity; a study in the origin, development, and classification of plant societies. Bor. GAZ. 31:73-108, 145-182. 1901.

------, The causes of vegetative cycles. Bor. GAZ. 51:161-183. 1911. WHITFORD, H. N., Genetic development of the forests of northern Michigan; a study in physiographic ecology. BOT. GAZ. 31: 289-325. 1901. FULLER, G. D., Evaporation and plant succession. Bor. GAZ. 52:193-208. 1911. tions. Bor. GAz. 58:193-233. 1914.

LIVINGSTON, B. E., The relation of soils to natural vegetation in Roscommon and Crawford counties, Michigan. BOT. GAZ. 39:22-41. 1905. ² TAYLOR, NORMAN, Flora of the vicinity of New York. Mem. N.Y. Bot. Garden 5: 1915, especially pp. 8-25. 59] Botanical Gazette, vol. 61

physics, chemistry, and bacteriology of soils outside of cultivated lands, and of the response of plants to their environment, is yet in a very rudimentary stage. Hitherto the tendency has been to consider one or two factors as an integration of many others, and to measure quantitatively only these two. For example, evaporation has been measured as an integration of all climatic factors, and soil moisture as an integration of all soil factors. It would not be surprising, therefore, if future progress should reveal some important factor which had been unavoidably overlooked. In view

of the present uncertainty concerning the relation between pine and oak, the following notes on the pine and oak of Long Island may be of interest. They are based only on observation, without quantitative measurements, and lay no claims to definite conclusions.

The locality in which these observations were made is that part of the outwash plain about four miles east of Hempstead and four miles south of Hicksville. Here are found a number of different kinds of forests: a small body of pitch pine (*Pinus rigida* Mill.), practically untouched except for the usual fires, stands of mixed oak and pine, an oak forest, and more stands of pine. On this small area of not over 80 acres are exhibited more interesting

problems than it has ever been the writer's good fortune to see on an area of the same size.

The first piece of forest which attracts attention is the body of pitch pine in its natural condition except for fires. The stand is composed of pure, even-aged pine, much damaged by fire. The trees, though about mature, as indicated by the flattening crowns, are only about 12 inches in diameter at breast height, by about 30 feet high. The understory is predominantly scrub oak (Quercus nana Sarg.), which is dense where the pine is open, diminishing where the canopy is more complete. In the scrub oak is a scattering of white oak (Q. alba Linn.), scarlet oak (Q. coccinea Moench.), black oak (Q. velutina Lam.), and post oak (Q. minor [Marsh.] Sargent). These oaks do not reach up into the main canopy and are short and limby. There was no pine reproduction, probably on account of the fires; fire-killed pine seedlings were found, and it is likely that many more had been entirely consumed.

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The soil is a light brown, pebbly sand of coarse texture, with the upper 2-3 inches darkened by humus. The glacial origin of this soil is attested by the planed surfaces of the pebbles. In one place where the pine bordered an open field, a small piece, not over 50 by 100 feet, had been clear-cut sometime ago, perhaps 15 or 20 years. Here the ground has been taken possession of by aspen, on the field edge of which is a little gray birch (*Betula populifolia* Marsh.), considerable white oak and black oak, and a little post oak; scrub

oak is mixed thickly with the aspen. The soil here was found to contain a considerable amount of clay or fine silty material.

That the clay or fine silty material is the cause of the aspen cannot be stated definitely, for the pine was there before the aspen, and might again take possession, as shown by pine seedlings on spots which had escaped fire. Furthermore, in another part of the forest, where the pine formed a fairly full stand except for occasional small openings made by trees which had been weakened by fire and then killed by insects, occur young aspen, gray birch, and sycamore (Platanus occidentalis Linn.). The soil here, at least down to 10 inches in depth, is the same coarse sand without clay as was found under the other parts of the pine forest; but, owing to the closer canopy of pine, there was a better mulch of needles, and a considerable quantity of humus in the first 4 inches of soil. It might be deduced that the extra mulch and humus here served the purpose of the clay, but it is dangerous to jump at conclusions from such observations. Clay might lie at various depths, being near enough to influence the vegetation in some places and not in others. Clay 2 feet below the surface would be sufficient to account for this second case of aspen and other deciduous trees. Judgment in this case must be withheld, therefore, until after further investigation.

Not far from this first body of pine, separated from it by a cultivated field, we find an open stand of pitch pine in which are scattered mature white oak trees, the understory being scrub oak. The white oak appears to be about the same age as the pine, but less numerous. The original stand, before fires became so frequent, was probably chiefly pine with a scattering of white oak. Here is what might appear at first sight to be an indication of

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succession, the oak replacing the pine; but the soil, though still a coarse sand, has a distinct trace of clay which could account for the presence of the oak.

A short distance from the pine and scattering oak just noticed, we find an open stand of short limby white oak with an occasional pitch pine. There is an understory of scrub oak, which is, however, far less dense than on the areas where the pine predominates. To all appearances this could be another stage in the succession from pine to oak, a stage somewhat later than the one noticed just previously, for here the oak predominates instead of the pine, while the pine now occurs only sparsely, as the oak had done in the other place. This idea finds support in the first examination of the soil, which proves to be the same coarse sand as that found under the first forest of pure pine; but deeper digging shows that only the first 6 inches are sand, while below the sand is clay. This clay amply accounts for the presence of the oak, and probably the surface layer of sand accounts for the scattering pine.

Adjoining the white oak and scattered pine just described is a typical oak forest. The trees are scarlet oak and white oak, chiefly the former, with a little black oak, an occasional small hickory, and in certain parts of the forest a little chestnut oak (Quercus prinus Linn.). There is no chestnut (Castanea dentata Marsh.). One old pitch pine (probably about the same age as the oaks) and a pine stub, which could easily have been taken for relicts of a former pine forest, were seen. There is also a little pine reproduction which probably will not come up unless the canopy is opened. The soil on which this oak forest is growing consists predominantly of clay or fine silty material. While not a very heavy soil, it was clearly one of moderately high moisture-retaining capacity. The precise nature of the differences between this soil and the coarse sand on which the pure pine was found cannot of course be stated without thorough analysis, but it is sufficiently clear that decided differences exist. This soil, so far as could be determined, strongly resembles that under the forest of oak with scattering pine, except that it lacks the surface layer of sand. It is significant that the layer of sand ends where the typical oak forest begins.

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In this case, at least, the conclusion appears unavoidable that the occurrence of pine and oak is attributable largely, if not primarily, to the occurrence of distinctly different soils. This does not mean that the factors tending to bring about a succession from pine to oak are absent, but merely that these factors appear in this case to be distinctly subordinate to the character of the soil. Only the most thorough quantitative investigation can begin to unravel all the factors involved, and final conclusions cannot be expected until further progress has been made in the sciences on which the investigation must be based, particularly in plant physiology and in physics, chemistry, and bacteriology of soils, all of which deal with the phenomena which go to make up the vegetative cover as we find it.

There is in this same locality another kind of succession, different from the physiographic one³ above referred to; this is a succession started by the interference of man.⁴

At the edge of the oak forest above described was found a patch of young pitch pine about 20 years old. The soil proved to be more gravelly than under the oaks, but with still a considerable proportion of clay or fine silty material. It might appear offhand from this that the clays do not necessarily support oaks; but the true explanation fails to corroborate this idea, and is very simple. Further examination revealed old, almost obliterated furrow marks, showing that this land had formerly been cleared and cultivated. That it originally supported oak was indicated by a strip of oak standing between the pines and a field still used for growing hay, and still further by a sharp line of demarcation between an old forest of oak and the young pine. There is but little scrub oak among the pines, and the better oaks, scarlet oak, black oak, and white oak, are coming in on the edges. It is obvious, therefore, that the pine is merely a temporary cover which has taken possession of the land after the oaks had been completely cleared off (not merely clear-cut), and the land later abandoned. If further evidence that pine is a forerunner of the forest on cleared and ³ COWLES, H. C., A textbook of botany. Vol. II. Ecology, p. 940. New York. 1911; also citations under note 1. 4 _____, op. cit., p. 958.

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abandoned land in this locality were needed, it is furnished by a few seedlings of pine in the neighboring hay field. The indications are that this entire locality was once covered with pine, and that on the better soils (those with more clay) the pine soon gave way to oak. Unquestionably the oak stage was reached on these better soils many years ago, probably not long after the oak forest had become established on the near-by hills to the north. But when, through the interference of man, the oaks are completely destroyed, as in clearing land for farming, and when the land is again abandoned, pine takes possession. The reason is probably to be found in the more rapid methods of seed dissemination possessed by the pine as compared with the oaks. This would account for the presence of gray birch, and occasionally aspen, on lands beginning to revert to forest. When the forest is cut for wood, and the stumps are left to coppice, the pine has another but far less favorable opportunity to establish itself. From observations on other areas, it seems that after cutting, provided no fire occurs, a considerable number of pine seedlings come in, but with a few exceptions are unable to develop on account of the more rapidly growing oak sprouts. The exceptions are probably seedlings which happen to grow in larger openings among the sprouts, or near old stumps which fail to sprout. Such exceptions readily account for the pines which, as noted above, might have been considered as relicts in the oak forest; for this forest, or rather the generation preceding it, had unquestionably been cut over for wood some 50 years ago. It is evident then that we have here two forms of pine forest: (r) a temporary form which will be replaced by an oak forest in a comparatively short time, roughly 150-300 years or possibly longer, depending a great deal on the size of the area; and (2) another form of which much less is known. The temporary form occurs on soils containing clay; the other form on sands. The question is: Will this second form occurring on sands be replaced by oaks

through an amelioration of edaphic conditions brought about by the pine forest itself? The tendency, on the strength of all the quantitative investigations of the subject to date, would be to answer yes. Such an answer would be most unfortunate in creating a bias in

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future investigations; and it is just this feature of the situation which needs emphasis. Conclusions from one locality should not influence investigations in another locality, except in creating a desire to test the conclusions. The answer should be: We do not, and cannot, know until after thorough quantitative study of all factors which so far as now understood may have a bearing on the question.

Meanwhile, until such an investigation is made, several features

of the situation, so far as they can be determined by observation without detailed study, may be noted. It is conceivable that, if conditions were left undisturbed for a sufficient length of time, the pine would, by a gradual accumulation of humus, render the soil favorable to the oaks,⁵ which would then crowd out the pine. But in nature, conditions, at least in forests, are never left undisturbed indefinitely, for if man does not start fires lightning will, and fire tends to produce a deadlock between the pine and the oak. It favors the oak against the pine in that the oak seedlings which are killed can come up again from sprouts, whereas the pine seedlings cannot. On the other hand, it favors the pine against the oak by destroying the physical conditions, especially the litter and humus,⁶ favorable to the oak. The result is that a worthless form of oak, the scrub oak (Quercus nana), which both is fire-resistant and can grow on sandy soil, takes possession of the ground. Above the scrub oak is seen an occasional pine or an oak, most frequently a white oak, owing to its greater power of fire-resistance. It might be noted here that the scrub oak, owing to its dense habit of growth, protects the soil against leaching out, as well as serving as an excellent accumulator of humus. It appears to be analogous to the snowbrush and manzanita in the northern and central Sierras of California. These species and their associates, which should not be confused with the true chaparral farther south, form a dense cover of brush about 4-8 feet high, which keeps the soil and lower atmospheric strata favorable for the establishment

⁵ By oaks is meant the forest-forming species, not the scrub oak (Quercus nana Sarg.). ⁶ It has been found by R. C. HAWLEY by quantitative experiments that repeated fires actually burn not only the surface mulch, but the humus which is in the soil.

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of the white fir (Abies concolor). This tree, owing to its ability to endure shade, persists under the brush, eventually forces its way through, shades out the brush, and reestablishes forest conditions. The difference is that the region in question possesses no trees as tolerant of shade as the white fir. At the same time, the scrub oak is never as dense as the Sierra brush, and offers in between clumps openings in which the pine or better oaks can come up. The pine, owing to its wider area of seed dissemination, has more opportunity than the oaks to take advantage of these openings, provided seed trees remain. On the other hand, the oak, when once it starts, stands a better chance of becoming established on account of its power to sprout after being killed by fire. The foregoing, though by no means covering the whole case, seems sufficient to show that the problem of succession so far as pine and oak are concerned is extremely complex. It is of the utmost importance that each case be considered by itself. So many complex and interacting factors, such as the previous history of the region (as emphasized by TAYLOR), the surrounding vegetation, and the soil and moisture conditions, enter into each case that the conclusions of one locality may be wholly misleading when applied to another locality only a few miles distant.

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